PROPRIOCEPTION IN THE LEGS OF PHALANGIDS

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The presence of thin areas in the exoskeleton of certain arachnids and other arthropods has been known for about 80 years. The thin areas, made up of epicuticle, are usually bordered by a thickened lamella and occur in two general shapes—slit-like and circular. Isolated, slit-like thin areas were noted by Bertkau (1878), while groups of more or less parallel slits resembled the ancient stringed instrument, the lyre, and prompted the term, "lyriform organs" (Gaubert, 1890). The circular ones were first described by Berlese (1909) and called "campaniform sensillae." Typically, the dendritic process of a bipolar neuron is attached to the epicuticle or to the bordering lamella. Snodgrass (1935) and Kaston (1935) have summarized the histology of the former condition in insects. In 1938 Pringle presented evidence from the cockroach that indicated stress reception as the real function.

Recently, the attachment of the neurite to the bordering lamella has been described with electron micrographs by Salpeter and Walcott (1960), and shown to function as a vibration receptor in spiders. The neurite is stimulated by stretching in the region of attachment to the epicuticle. Most commonly this is done by compression pressure on the bordering lamella. This results in exaggerating the convexity of the epicuticle.

These organs exhibit considerable morphological variation and have been reported in insects, spiders, scorpions, mites, ticks and phalangids (Gaubert, 1892; Hansen, 1893; Hansen and Sorensen, 1904). The present paper illustrates campaniform and slit organs (isolated, grouped, and lyriform) of phalangids and reports evidence suggesting the function of at least the campaniform organs to be proprioceptive.

PROCEDURE AND RESULTS

Legs of phalangids possess several shapes and combinations of sensillar organs. The location and number on each of the four legs for six species are indicated in Table I. Considerable similarity exists among all of the species shown except *Caddo agilis*. In addition to the sensillar arrangement, this form is distinguished from the others in Table I by size, habitat and morphology.

Data for all the leg segments are included except for the coxa. On this segment, typically a single slit sensillium occurs on the distal margin. At the distal margin of the trochanter there occurs, except in *Caddo*, a lyriform organ with a fairly constant number of slits—seven, for example, in *Phalangium opilio* (Fig. 1). Small clusters of I- and L-shaped slit sensillae occur on the proximal portion of the femur (Figs. 1 and 2). The leg autotomy plane is located between the trochanter and femur. Presumably, the rich sensillar supply on these segments functions to indicate to the animal mechanical stress upon this plane. Large, single slits are

TABLE I

Location and number of proprioceptor organs on the legs of certain phalangids

Leg segment	Caddo agilis Leg number				Opilio parietinus Leg number				Phalangium opilio Leg number			
	1	2	3	4	1	2	3	4	1	2	3	4
Trochanter	0	0	0	0	4	2	4	5	7	7	7	7
Femur—P*	9	9	9	5	18	16	22	21	29	30	30	29
—S*	1	1	1	1	2	4	2	2	4	5	4	4
—D*	1	1	1	1	1	1	1	1	1	1	1	1
Tibia—P*	2	?	2	2	6	3	6	6	9	8	8	9
Metatar. P*					7	5	7	7	9	9	8	9
Tarsus 1st*					1		1		1(2)	1(2)	1	1(2)
Mid.*							6	6	7–12	11–14	9–10	7–11

Leg segment	Leiobunum calcar Leg number				Leiobunum longipes Leg number				Leiobunum politum Leg number			
	1	2	3	4	1	2	3	4	1	2	3	4
Trochanter	5	5	5	5	6	7	7	5	5	5	4	6
Femur—P*	21	24	23	24	30	31	30	27	23	27	22	29
—S*	4	5	4	5	4	5	4	4	3	5	4	4
—D*	1	1	1	1	1	1	1	1	1	1	1	1
Tibia—P*	7	5	5	7	7	7	7	6	7	7	7	9
Metatar. P*	8	6	7	8	8	8	8	8	8	10	8	10
Tarsus 1st*	1	1	1	1	1	0	1	1–2	1	1	1	1
Mid.*	7	7	8	6–8	8–11	13–16	6–10	10–11	4	9	6	7–8

* Key to symbols:

    P—organs located on proximal portion of leg segment.
    S—shank of leg segment.
    D—distal portion of leg segment.
    1st—number of organs found on the most proximal article of tarsus.
    Mid.—the number of the article on which is found a campaniform organ. Extremes (for example, 7–12) indicate that organs have been found on articles within these limits.

more or less evenly spaced along the shaft of the femur. The largest slit organ on the leg occurs on the distal femur where it articulates with the patella (Fig. 3). The ventral, proximal portion of the tibia has a cluster of campaniform sensillae. Usually, three slit organs and three to seven campaniform sensillae occur on the dorsal surface of the metatarsus near the articulation with the tibia. Occasionally one or two of these latter organs are separated and distal from the cluster. Typically, two solitary campaniform organs are found on the tarsus; one is on the proximal-most article and the other on an article in the middle one-third of this segment (Fig. 4). Observations of the organs tabulated in Table I were made from exuviae of the final molt.

Although Savory (1962) and others have indicated that the second pair of legs possess special senses, the arrangement and kinds of sensillar organs listed in Table I do not show any consistent disparity with the other three pairs. Legs from all four pairs were used in the experimentation; however, no differences be-
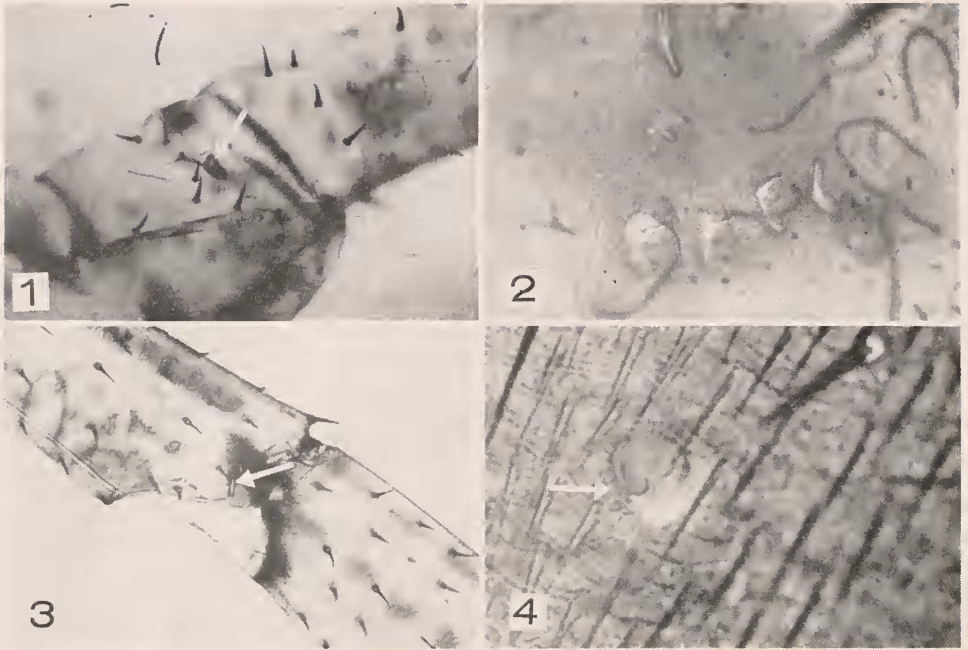
FIGURE 1. Lyriform organ at distal margin of trochanter (arrow). The autotomy plane which separates trochanter from femur is shown under the other end of the arrow. A cluster of I- and L-shaped slit organs may be seen on the proximal portion of the femur (right).

FIGURE 2. Several slit organs clustered at base of femur (see Figure 1). The expanded area in the middle of the slit probably receives the attachment of a bipolar neuron.

FIGURE 3. Large, thick-bordered slit organ on femur (arrow) where femur articulates with patella.

FIGURE 4. Campaniform sensillium on twelfth article of the tarsus; the structure measures approximately 20 by 15 microns. Figures 1–4 are photographs made from molt cases of *Phalangium opilio* L.

tween legs were observed in the records obtained. Oscilloscope traces shown in Figures 5–7 were obtained from the left leg I of *Phalangium opilio*.

Legs from healthy adults were removed at the autotomy plane between the trochanter and femur and mounted upon a Plasticene support. Platinum wire electrodes inserted into the open, proximal end and the patellar end of the femur were connected via a Grass Type P. 4 preamplifier to a Tektronix 531 oscilloscope.

By adequate support of all sections of the leg except the test area, stress could be placed on specific sensillae. Stress was produced by hyperextending or hyper-flexing the normal angle of movement at an articulation nearest the sense organ. This was done by manually-operated glass and steel probes.

Although pressure was applied on all joints of the leg, action potentials were consistently obtained only upon hyperextension of the tibiometatarsal joint (Fig. 5) and hyperflexion of the tarsometatarsal joint (Fig. 6) and tarsal articles. Adaptation was rapid and complete.

To localize the site of origin of the nervous activity shown in Figures 5 and 6,
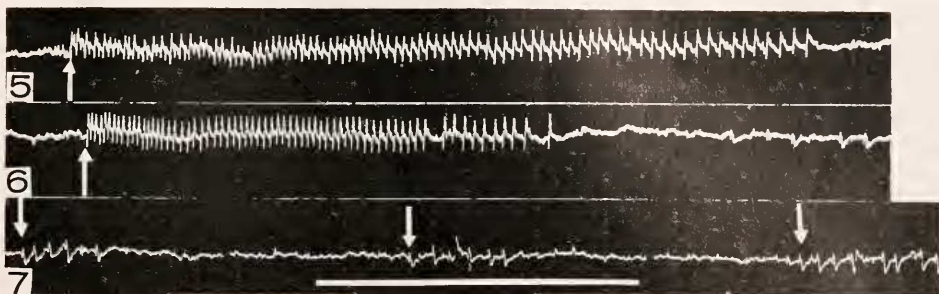
Figures 5 and 6. Oscilloscope records from leg nerve at the femur. Figure 5. Forced extension of the tibiometatarsal joint of *P. opilio* L. Figure 6. Forced flexion of a tarsometatarsal joint of the same species. Arrows indicate time at which stress was applied.

Figure 7. Three oscilloscope records of extension of tarsometatarsal joint. The typical pattern of this trace may be seen in Figure 6 near the right-hand side. Arrows indicate the moment of flexing; the time bar shows one-second interval on Figures 5, 6 and 7.

articles of the tarsus and metatarsus were removed, a few at a time, by cutting. Impulses continued to be elicited, upon stress, in a normal manner until the immediate region of a sensillium was removed; then the record ceased. Local destruction attempts were unsuccessful.

A series of differently-shaped impulse discharges usually appeared on the record about 0.4 second after adaptation (Fig. 6). It was interesting to note that a wave form which had a similar shape appeared upon moving the leg segment in the direction opposite to that producing the stress discharges and without exceeding the normal limits of movement. Figure 7 indicates three such records from extension of the tarsometatarsal. Just where this second discharge originated is unknown, possibly in a different sense organ located nearby, or perhaps two neurons are associated with the same sensillium to transmit "action" and "reaction" stimuli. However, morphological descriptions known to the writer have shown only one nerve cell involved for each organ.

Attempts to induce distinct responses from the grouped slits (Figs. 1 and 2) generally failed. However, surface pressure from careful scraping of the area with glass and steel probes resulted in a jumble of electrical activity. When nearby spines were intentionally prodded, no response was obtained. This was sufficient to suggest that impulses were coming from the slit organs. These manipulations were observed plainly under suitable magnification.

The slit sensillae of the femur, with one exception, have yielded no clear response to stimulation. On this one occasion it is believed that insertion of the electrode into the femoropatellar junction caused pressure to activate the large single slit sensillium at that joint (Fig. 3). Very regular, large, fast impulses continued for many minutes. They presumably did not originate from leg segments other than the femur since manipulation of these segments caused no alteration in the frequency or amplitude of these discharges. Subsequent repositioning of the femoropatellar electrode abolished the response. It is possible that one of the other sensillae located on the shank of the femur was the organ responding. This is unlikely, however, in that lateral movements of the shank, designed to place stress upon these organs, produced no response.

Response to parameters other than mechanoreception was sought. Sound waves from a tuning fork (100 cps) and loud noises resulted in no detectable response by the intact, functioning sensillae. Addition of xylene to the tarsal and metatarsal sensillae caused no observable response. These sense organs functioned typically before and after application of the xylene. Pringle (1955) used the application of liquid xylene on slit sensillae as a criterion of possible chemoreceptive sensitivity.

Discussion

The shape of phalangids is exaggerated as compared to that of most arthropods, and indeed other forms, in that the legs typically are extremely long and of small diameter compared to the small, oval body. Being without antennae the animal first encounters its environment predominately with its legs. For this reason, one might expect to find a variety of sensory organs here.

The legs are directed radially and upward from the animal in an arch so that the body is suspended in the middle third of the distance from the surface touched by the tarsi to the highest part of the arch of the leg. The body is therefore exposed only directly above and below. All joints of the legs operate essentially in one plane with respect to the body (dorso-ventral) except the trochanter-femur which, in combination with the coxa-trochanter, is capable of movement in a variety of dorso-ventral and anterio-posterior directions. It is at the femoro-trochanter junction that the leg may be autotomized. In nature, phalangids frequently are encountered with one or several legs missing. Legs grasped by predators or trapped during the molting process are readily shed in order to escape.

Sensillar supply is richest near this autotomy plane and diminishes to where the only type present on the distal half of the leg is the campaniform sensillium. These few isolated organs register stretch and compression pressure in the region of joints, i.e., between leg segments or between the hinge-like series of tarsal articles. Presumably, stress in other than the plane of the joint movement would be detected mainly in the region of the autotomy plane, where groups of slit sensillae are oriented so as to respond to deformation from any direction (Figs. 1 and 2). The campaniform organs detect shock stress coming from ventral (about the tibiometatarsal joint) and dorsal or ventral directions (about the metatarsotarsal joint and adjoining tarsal articles). These organs apparently do not function to indicate, to the animal, position of the appendage while at rest or from contacts with the relatively stationary aspects of the environment (forest litter, tree trunks, etc.) since action potentials are picked up only when the normal limits of the joint are exceeded. Hence, they function as well-distributed alarm systems which "go off" when the safety of the limb and probably the animal are threatened.

Summary

1. In the legs of phalangids thin areas in the exoskeleton occur in four basic arrangements: (a) solitary slit sensillae, (b) I- and L-shaped slits in clusters, (c) lyriform organs, and (d) circular or campaniform sensillae.

2. Evidence was obtained to indicate that at least the campaniform sensillae on the phalangid tarsus and metatarsus function as proprioceptors. Action poten-

tials, from grouped and isolated slit organs on the tibia and femur, were elicited but were less distinct as to electrical characteristics and function.

3. No response was seen upon application of sound waves and xylene to the campaniform sensillae.

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